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The Ovarian Cycle, Reproductive Potential, and Structure in a Population of the Japanese Lacertid *Takydromus tachydromoides*

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A three year study of a population of *Takydromus tachydromoides* in central Honshu, Japan revealed that yolk deposition in follicles of juvenile lizards begins in the late spring following their first hibernation, at a body length exceeding 41 mm. Adult females emerge from hibernation with yolked follicles. Oviposition of first year lizards begins in early June, reaches a maximum in July and ends before mid-August. Older females begin oviposition in early May, reach their peak in the first half of June, and cease laying in late July.

In experimental lizards corpora lutea regressed from an average of 2.1 mm on the day of oviposition to 1.0 mm five days postoviposition. These persist as corpora albicantia apparently for the life of the lizard. Estimates of age groupings by counts of corpora albicantia suggests that first year females contain none in spring and 4–13 in fall; second year lizards, 1–12 in spring and 14–26 in fall; third year females, 14–23 in spring and 26–39 in fall; and fourth year females, 31–40 in spring and 51–69 in fall. The incidence of corpora albicantia in adult lizards collected from 15 August until hibernation is 97%.

Clutch size of first year lizards ranges from 1 to 4 for all clutches, with means of 2.6 for the first clutch and 2.4 for the second and third. Clutches of second year females range from 1 to 6, with means of 4.0 for the first and second, and 3.4 for the third clutch. Third year females lay clutches of 1–7 ova, with means of 4.4 and 5.1 for first and second clutches, respectively; third clutches approximate 3.5 eggs. Fourth year females apparently deposit 4–6 ova or more per clutch.

Mean clutch number calculated by dividing average clutch size into the mean number of corpora albicantia in fall lizards is 2.9. A mean clutch number of 2.7 was obtained by dividing the length of the reproductive season by the time required to produce the first clutch. The reproductive season varied from 76 to 86 days for first year females, and from 112 to 127 days for older females.

Reproductive potentials estimated by counts of yolked follicles, corpora lutea and oviductal eggs were 7.4, 11.4, and 12.8, for first, second and third year females, respectively. Estimated from the mean difference between counts of corpora albicantia in spring and fall lizards, they were 9.3, 12.9 and 11.6, in respective order. The latter method suggests a mean reproductive potential for fourth year females of 20.4.

There is no difference in average clutch size between small and large females of the same age group, but second year females produce first clutches nearly twice as large as those of first year lizards. Average weights of individual eggs and total clutches increase as females age. Total clutch weight ranges from 30 to 50% of the females postovipositional weight.

The sex ratio in all age groups in each season is 1:1. Of the total female sample, 62.5% had survived their first breeding season, 25.0% their second, 9.8% their third, and 2.7% their fourth season.

Introduction

The genus *Takydromus* (Lacertidae) is distributed in eastern and southeastern Asia from the northernmost Japanese island of Hokkaido through Korea, mainland China, the Ryukyu Islands and Taiwan, and down the Malaysian peninsula at least to Java (De Rooij, 1915:155). Throughout this broad area of north temperate, subtropical and tropical habitats extending over some 54° of

Fig. 1. Study area at Hanno, Saitama Prefecture, Japan. April 1967.

latitude, all members of the genus, where habits are known, exhibit a preference for grassy situations.

The little information available on the biology of this genus pertains largely to the most northerly ranging species, the kanahebi, *T. tachydromoides* Schlegel. Virtually nothing is known of the subtropical and tropical species. The distribution of *T. tachydromoides* has been considered by Stejneger (1907), Boulenger (1917), Slevin (1930, 1937), and Okada (1933, 1938). Minobe (1927) presented data on diet and casual observations of habits and reproduction. Inukai (1930) superficially described the reproductive cycle of lizards purportedly from central and northern Japan, while Ishihara (1964) reported more detailed observations on breeding habits from captive *T. tachydromoides* in the Kyoto area. A number of papers by Japanese workers deal with experimental studies on the effects of gonadectomy, on hormonal administration, embryology and morphology. There has been no thorough study published in English or Japanese on the ecology of this species.

While in Japan from 1956 to 1959, I became familiar with *T. tachydromoides* and recognized its suitability for a population study. In March 1965, I began a project to determine whether seasonal fluctuations in liver and fat body weights, and seasonal variations in parasite infection rates might be correlated. Soon it became apparent that great quantities of additional biological data could be obtained simultaneously. Between March 1965 and November 1967, a period spanning three complete annual reproductive cycles, 2172 lizards were collected from various localities in central Honshu; all but 18 of these were from the Kanto Plain. Approximately 1500 (69%) were autopsied, with the remainder, mostly juveniles, utilized for experimental work. Of these 1500 autopsies, 1253 lizards were collected from a single local population. Data obtained during this period will form the basis for this and subsequent reports.

Materials and Methods

Locality.—An area of hillside paddy fields near the town of Hanno, Saitama Prefecture, Honshu (45 km WNW of Tokyo), was selected as the study area. All data presented herein, except for measurements of laboratory clutches, were obtained from the Hanno population. Most lizards of the laboratory colony were collected in one of the Tokyo suburbs, in the vicinity of Igusa, Suginami Ward.

Habitat.—Field work was conducted in and about several paddy fields in valleys separated by densely wooded ridges (Fig. 1) on the slopes of a small mountain, Asahi-yama (el. 218 m). Lizard density was greatest along field margins, and lessened distinctly on the slopes. Some lizards, however, were resident in less densely wooded or cut-over areas on the ridge crests, so it may be presumed that no barrier to gene flow exists among the various demes inhabiting the annectant valleys. Since this species apparently has a very small home range (Ishihara, 1965 oral presentation), it is inprobable that an individual lizard hatched in one valley ever migrates into another.

On the ridges, conifers and hardwoods

were dominant, with grasses rapidly filling cut-over areas. Hardwoods and deciduous shrubs extended along the ridge slopes to within several meters of the field margins, and hibernacula occurred along these slopes. Along the field margins were abundant grasses which grew rapidly in spring to reach a maximum height in July and August, after which they were usually cut in preparation for rice-harvesting in late September and early October. The paddy fields laid fallow from mid-October to early April, when they were prepared again for planting. These particular fields had probably been under continuous cultivation for 200–300 years.

Sampling design.—Collecting was planned to provide a minimum sample of 25 first year and 25 older lizards monthly, from emergence in late March to hibernation in late October. This schedule was adhered to except in July and August, the period of minimum population density (and maximal environmental discomfort), when it usually proved impossible to collect enough lizards. Collecting was by hand and noose, and all lizards seen were recorded. Two adjacent valleys, sites 1 and 2, were collected every month, furnishing 1073 lizards in 62 collecting trips. Actual time spent in traversing the same route through sites 1 and 2 averaged about 2.5 hr. During spring and fall, collecting commenced at 1030 hr. From June through August, collecting began at 0830 hr, as lizards were observed to commence and cease their daily activity earlier. Three other valleys were used as control areas to determine whether such intensive collecting modified any of the population characteristics of the kanahebi or its parasites. Site 3 furnished a total of 54 lizards in July and October, 1966 and April 1967; 37 lizards were collected in site 4 in June 1967; and 89 were taken from site 5 in September and October 1967. As no differences appeared in reproductive characteristics, all specimens collected in the five valleys and along the ridges near Hanno were used in the analysis of reproductive potential. However, only those specimens actually collected along the field margins and the adjacent slopes (up to 3 m distance) from sites 1 and 2 were used for estimates of population structure.

Processing of material.—All lizards collected were refrigerated, at approximately 6° C, immediately upon return from the field. Unaltered stomach contents support my belief that metabolism was sufficiently diminished to produce no significant change in the specimens before dissection. Within one week of capture, specimens were killed with Nembutal and measured with a plastic mm ruler, digestive tracts were removed, livers and fat bodies weighed, viscera and coelom examined, and bodies preserved in formalin. Gonads destined for sectioning were preserved in Bouin's fixative. All measurements of gonads were obtained from formalin-fixed specimens preserved in 30% isopropyl alcohol. Deposited ova were measured with calipers, while all other measurements were made with an ocular micrometer. In analysis of data, the levels of significance chosen were .05 (significant) and .01 (highly significant).

Estimation of age.—Throughout this study, age estimates for females were based upon the number of corpora albicantia present in the ovary. First year lizards contained no corpora albicantia in spring and 4–13 in fall. These females could also be separated by body size. Second year lizards had 1–12 in spring, and 14–26 in fall. Corpora albicantia in third year lizards numbered 14–23 in spring, and 26–39 in fall. Lizards with 31–40 in spring and 51–69 in fall were considered to be fourth year.

Ovarian Cycle

Growth and Development of Ovarian Follicles in First Year Lizards

Follicle growth.—Kanahebi hatchlings are approximately 22 mm snout–vent. Between 22 and 27 mm, ovaries can be distinguished. Follicles are minute, 0.1–0.3 mm in diameter, and numbered two or three in each ovary. Lizards that reach a length of 30–32 mm in September may have 2–4 follicles in each ovary that exceed 0.3 mm in size, with an average diameter close to 0.3 mm. In October and November, prior to hibernation, hatchlings between 31 and 36 mm have four or five follicles per ovary that exceed 0.3 mm ($\bar{x}$ about 0.6 mm). Growth ceases during hibernation from November to March. Lizards 32–33 mm at the end of March have 4–6 follicles per ovary exceeding 0.3 mm, with the average diameter still 0.6 mm. In April and May growth rate is greatest, but some lizards still do not exceed 33 mm body length. In these, 2–5 follicles per ovary exceed 0.3 mm, with the average diameter remaining about 0.6 mm. April and May lizards attaining body lengths of 34–40 mm have 3–8 follicles

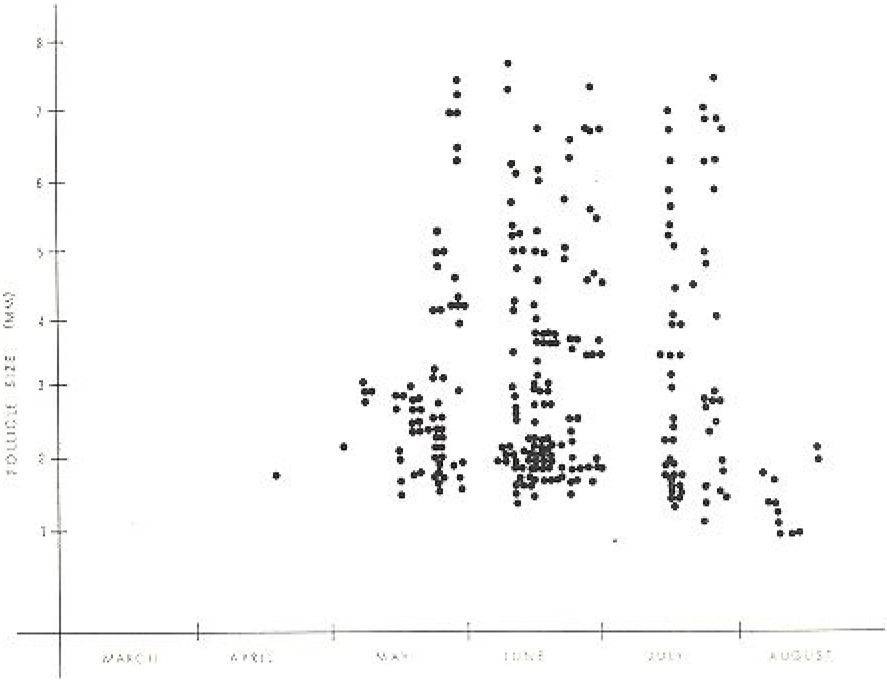

Fig. 2. Size of yolked follicles in first year lizards.

per ovary exceeding 0.3 mm, while the average diameter has increased to about 0.8 mm. First year lizards 42–43 mm in mid-May may still lack yolked follicles; each ovary, however, will contain 6 to 8 follicles averaging 1.0 mm in diameter.

Yolk deposition.—In first year lizards, yolk deposition does not occur until the lizard attains a minimum snout-vent length of 41 mm. The average size at which yolk deposition begins is somewhat larger: a series of nine nonparous first year lizards with yolked follicles less than 2.0 mm (1.4–1.9, $\bar{x}$ 1.76 mm) ranged in body length from 43 to 50 mm, $\bar{x}$ 45.7 mm.

The smallest yolked follicles observed were 1.0 mm in diameter. These were in multiparous first year lizards, and the condition of parity perhaps influences yolk deposition. Yolk deposition in follicles destined for successive oviposition does occur in first year lizards, though not commonly: four of 85 (4.7%) first year lizards collected before August contained yolked follicles of greatly differing sizes.

Ovulation.—Yolked follicles increase in size to reach a maximum diameter of 7.6 mm in first year lizards, at which time ovulation evidently occurs. No unshelled, ovulated ova were present in first year females. While measurements of oviductal eggs in preserved lizards are unreliable because of the probability of mechanical deformation, it is worth noting that the three smallest shelled eggs in oviducts of two first year lizards were 7.5, 7.6 and 7.7 mm in length.

Monthly distribution of yolked follicles.—Fig. 2 reveals that yolked follicles in first year lizards usually appear from mid to late May, but only occasionally from April to early May. The onset of yolk deposition in first year females clearly is closely correlated with growth rate. Some slight differences in the monthly distribution of yolked follicles were found among the three seasons sampled (Table 1).

The largest follicles were found in the last week of May–first week of June; third–

Table 1. Monthly Incidence of Yolked Follicles in First Year Lizards.

Yr. hatched	% of sample with yolked follicles in					
	Mar.	Apr.	May	June	July	Aug.
1964	0	10	14	100	100	50
1965	0	0	41	90	86	0
1966	0	0	53	100	80	33

TABLE 2. MONTHLY INCIDENCE OF OVIDUCTAL EGGS AND CORPORA LUTEA IN FIRST YEAR LIZARDS.

% of sample with	Mar.	Apr.	May	June 1–15	June 16–30	July	Aug. 1–15	Aug. 16–31	Sept.–Nov.
Oviductal eggs	0	0	0	24	24	41	6	0	0
Corpora lutea	0	0	0	10	43	52	63	0	0
Either eggs or corpora lutea	0	0	0	33	67	93	69	0	0

fourth weeks of June; and third–fourth weeks of July. Those yolked follicles present in August probably represent potential atresia; none exceeded 2.1 mm in diameter.

Oviposition.—Criteria useful in determining periods of oviposition are the presence of oviductal eggs or corpora lutea (Table 2).

These data indicate that oviposition of first year lizards begins in early June, reaches its peak in July, and terminates before mid-August. The conclusions fit well with the data on yolked follicles presented above: largest yolked follicles in late May–early June, last two weeks of June, and last two weeks of July. The smallest lizard bearing evidence of successful oviposition was a 43 mm female collected 11 August 1965, containing six corpora lutea.

Corpora lutea and corpora albicantia.—The corpus luteum is a circular to oval structure which resembles, when not mechanically compressed, a doughnut. Its color ranges from reddish, in probably recently ovulated lizards, to cream or white. As it regresses, it turns yellow and deepens finally to bright orange. The size at which the orange hue appears varies, but it is in the vicinity of 1.0 mm. Some 1 mm corpora are still yellow, but most are orange. I have selected this color change as the criterion for classification of corpora as corpora albicantia. Corpora albicantia may shrink slightly more, to about .3–.5 mm, but do not regress completely, persisting apparently for the life of the lizard. Evidence for persistence will appear below.

To obtain data on the regression rate of the corpus luteum, ten gravid first year and five older laboratory colony females were maintained at 25° C for varying periods following oviposition. Clutch size was recorded for each, and lizards were killed at intervals, starting with the day of oviposition. Data obtained are presented in Fig. 3, with measurements of corpora lutea present in 55 field collected females containing oviductal eggs. In gravid females, corpora lutea averaged 2.4 mm, and ranged from 1.9 to 3.0 mm. A laboratory female killed on the day of oviposition contained corpora lutea averaging 2.1 mm. Corpora lutea in all females killed five days or more after oviposition were approximately 1.0 mm in diameter, except for a single female killed at 18 days which contained corpora lutea averaging 1.7 mm. At 60 days corpora lutea were 1.0 mm in diameter and deep yellow. At 108 days, the final female contained corpora which were 0.7 mm in mean size and bright orange in color. If the regression rate in nature is similar to that found in this experiment, females collected with corpora lutea exceeding 1.2 mm

TABLE 3. CLUTCH SIZES ESTIMATED BY ALL METHODS.

♀ age (yr)	Clutch No.	Yr of collection: 1965 range	1965 $\bar{x}$	1966 range	1966 $\bar{x}$	1967 range	1967 $\bar{x}$	Estimate based on total sample: range	$\bar{x}$
1st	1	1–4	2.6	1–4	2.5	1–4	2.7	1–4	2.6
	2	2–4	2.7	1–4	2.5	1–4	2.7	1–4	2.6
	3	2–4	2.8	2–4	2.7	1–3	2.0	1–4	2.5
2d	1	2–5	3.7	2–6	4.2	2–5	4.0	2–6	4.0
	2	3–4	3.8	2–5	3.7	3–6	3.8	2–6	3.8
	3	2–6	3.5	2–3	2.8	4–5	4.5	2–6	3.4
3d	1	1–5	3.6	3–6	4.5	4–6	5.0	1–6	4.4
	2	4–7	5.3	4–6	4.9	4–6	5.0	4–7	5.1

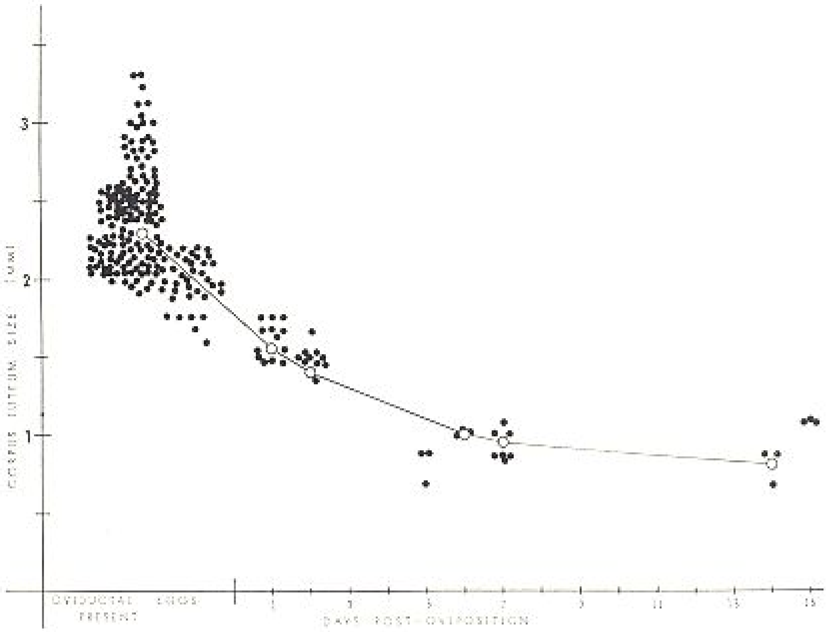

Fig. 3. Regression in size of corpora lutea among laboratory lizards. Hollow circles represent means, solid circles are individual corpora lutea. Line fitted by eye.

in diameter should have oviposited within the previous week.

As indicated above, corpora lutea appear in first year lizards in early June, while those last seen are within the first half of August. They are present in 10% of the early June sample. Corpora albicantia, on the other hand, appear in the last two weeks of June and their incidence rises to 97% in those lizards collected from 15 August to hibernation. The percentage (14%) of late June lizards with corpora albicantia corresponds well to the presence of corpora lutea in 10% of the early June sample, which suggests that regression actually occurs at a faster rate under natural conditions than in the laboratory.

Clutch Size and Number in First Year Lizards

Clutch size was estimated by three methods: the number of yolked follicles of similar size present; the number of corpora lutea; and the number of oviductal eggs present. Yolked follicles less than half the size of others present were presumed to belong to the next clutch. Estimation by corpora lutea counts is the most accurate method, as follicular atresia (see below) and oviposition of partial clutches may occur, and thereby affect the accuracy of estimates from yolked follicles and oviductal eggs respectively. As the discrepancy between estimation methods amounts to only 13% or less, the estimates given in the tables below are those obtained by combining all methods. Clutch number was determined by the presence, absence and size of corpora lutea and albicantia, and yolked follicles. For example, a female with no corpora albicantia, three corpora lutea and four yolked follicles of similar size obviously had produced a first clutch of three and was forming her second clutch of four eggs. Or a female with two corpora albicantia, three corpora lutea, and three yolked follicles contained evidence of three clutches, sized two, three and three.

Table 3 presents estimates of clutch sizes of first year females for each season, and an overall estimate of clutch sizes obtained by combining three years data.

Slight differences are apparent among the estimates for the three seasons, but none are significant.

Reproductive Potential of First Year Lizards

Estimates of clutch size obtained from counts of yolked follicles, corpora lutea and oviductal eggs, were used in the determination of reproductive potential. For comparison, counts of corpora albicantia present in

TABLE 4. ESTIMATES OF REPRODUCTIVE POTENTIAL BY TWO METHODS.

♀ age (yr)	yr collected	Estimation method: yolked follicles, corpora lutea and oviductal eggs		corpora albicantia in spring lizards		corpora albicantia in fall lizards		$\bar{x}$ difference between fall and spring lizards
		$\bar{x}$	max	$\bar{x}$	range	$\bar{x}$	range	
1st	1965	7.9	12	0	0	8.6	4–13	8.6
	1966	7.9	12	0	0	10.8	6–13	10.8
	1967	7.4	11	0	0	8.6	4–12	8.6
TOTAL SAMPLE		7.7	12	0	0	9.3	4–13	9.3
2d	1965	10.9	15	7.0	2–12	18.0	14–24	11.0
	1966	10.7	14	4.9	1–12	19.5	16–26	14.6
	1967	12.3	16	5.7	1–12	18.5	14–25	12.8
TOTAL SAMPLE		11.4	16	5.6	1–12	18.5	14–26	12.9
3d	1965	12.9	16	19.7	18–21	27.8	26–30	8.1
	1966	12.9	16	15.7	14–17	33.0	31–35	17.3
	1967	10.0	–	18.8	16–23	28.4	26–39	9.6
TOTAL SAMPLE		12.8	16	18.1	14–23	29.7	26–39	11.6

fall lizards following their first breeding season are included in Table 4.

Differences apparent between mean reproductive potential estimated by clutch size and the mean number of corpora albicantia in fall lizards are not significant.

OVARIAN CYCLE OF OLDER LIZARDS

Growth and development of ovarian follicles.—No differences are present in the numbers and sizes of unyolked follicles among lizards that have completed their first, second or third breeding seasons. The cycle of development, therefore, will be described using combined data from all older lizards.

Following the breeding season, lizards collected in August contained 8–22 unyolked follicles averaging 0.8 mm in diameter. In September, 13–25 follicles were present, averaging 0.9 mm. October lizards had 17–25 follicles (av. 0.9 mm), while two females collected in November had 20 follicles each ($\bar{x}$ 1.1 mm). After hibernation in March, follicles number about 20 ($\bar{x}$ 1.2 mm). In April, 14–16 unyolked follicles are present, with an average size of 1.0 mm. May lizards have 11–24 follicles, again averaging 1.0 mm. These data suggest that ovarian follicles increase in both number and size from a minimum following the breeding season to a maximum upon entry into hibernation. Following emergence from hibernation, yolk deposition occurs continuously throughout the spring and early summer, and both the number and size of yolked follicles declines slightly. The mean size (1.0 mm) for unyolked follicles in April and May is probably correlated with the minimum follicle size at which yolk deposition occurs.

Yolk deposition.—The pattern of yolk deposition in older females differs from that in first year lizards, where it is dependent upon attaining a certain minimum body size. Table 5 shows that 85% of older females con-

TABLE 5. MONTHLY INCIDENCE OF YOLKED FOLLICLES, OVIDUCTAL EGGS, CORPORA LUTEA, AND CORPORA ALBICANTIA IN OLDER LIZARDS.

% of sample with	Mar.	Apr.	May 1–15	May 16–31	June 1–15	June 16–30	July	Aug. 1–15	Aug 16–Nov.
Yolked follicles	85	92	100	95	100	88	100	0	0
Oviductal eggs	0	0	8	65	25	53	55	0	0
Corpora lutea	0	4	12	25	75	35	27	73	0
Either corpora lutea or oviductal eggs	0	4	19	90	100	88	82	73	0
Corpora albicantia	100	84	69	95	75	71	73	100	100

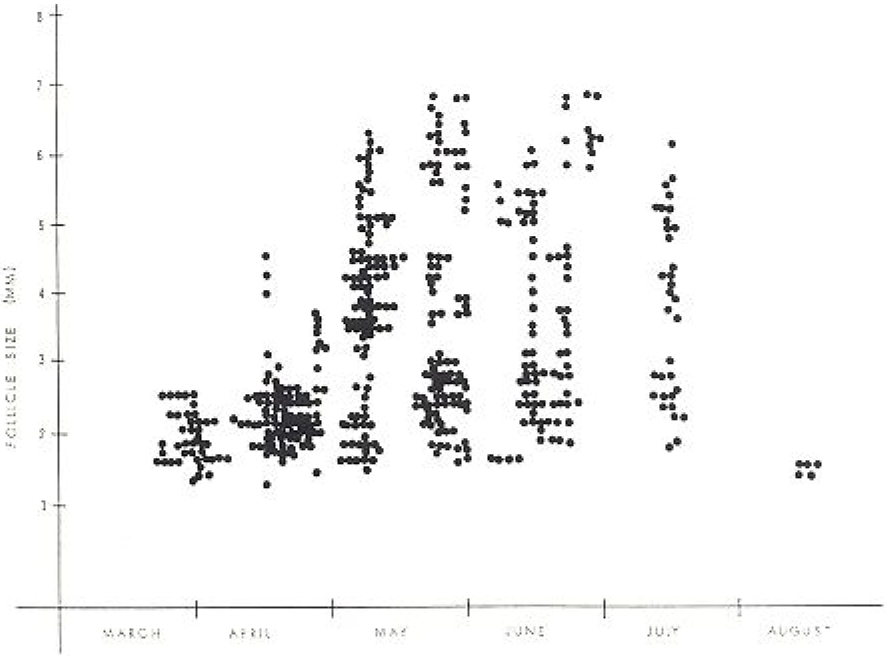

Fig. 4. Size of yolked follicles in older lizards.

tain yolked follicles upon emergence from hibernation in the last week of March.

The smallest yolked follicles were 1.1 mm in diameter, in a primiparous second year female collected in April. As in yearling females, yolk deposition in follicles destined for successive oviposition occurs: nine of 114 older females (7.9%) contained yolked follicles which clearly would not be ovulated at one time.

Ovulation.—In contrast to first year females where ovulation apparently occurs when yolked follicles reach a diameter of 7.6 mm, in older females the largest yolked follicles measured only 6.8 mm (Fig. 4). Again no unshelled ova were observed. As shown in Fig. 4, the largest yolked follicles were found in late May and late June, although follicles approximating 6 mm in size were present continually throughout May and June. Yolk deposition ends in mid-July. The smallest follicles present in July and the few found in August almost certainly are potentially atretic.

Oviposition.—Oviposition in older females begins in early May, a full month earlier than in first year lizards, reaches its peak in the first half of June, and terminates in late July (Table 5). Occasional females produce their first clutch of the season as early as April.

Corpora lutea and corpora albicantia.—The incidence of corpora lutea in older females rises after April to reach a peak in early June, then declines slightly before a second peak in early August, following the end of oviposition in late July. Corpora albicantia, however, decline in incidence in April and early May, rise in late May, remain level in June and July, then rise to a maximum in August (Table 5). The decline in incidence in certain months will be discussed below.

Clutch Size and Number in Older Lizards

Among older lizards, clutch size was estimated in the same manner as in yearling lizards. Table 3 presents data on clutch size of lizards containing less than 12 corpora albicantia, and presumably in their second breeding season. No significant annual differences are present among the data.

The reproductive potential of second year lizards was estimated from clutch sizes in the manner described for first year lizards. For comparison, counts of corpora albicantia in spring lizards prior to breeding, in fall lizards following breeding, and the difference in these counts are included in Table 4. Differences between the estimated reproductive potentials and the increases in corpora albicantia counts resulting from the second breeding season are not significant.

Lizards containing 14–23 corpora albicantia in spring were considered to be entering their third breeding season. No significant annual differences were found among the data in Table 3.

Data on third clutches of third year females are scanty, and available only from yolked follicles of lizards hatched in 1962 and 1963. None of the 1964 lizards collected in 1967 had evidence of third clutches. A third clutch present in one 1962 female consisted of four yolked follicles. Four 1963 females contained third clutches of three or four yolked follicles, with a mean of 3.5.

The estimate of reproductive potential (Table 4) for 1964 lizards in their third breeding season (1967) includes only clutches one and two, for a total of ten eggs. As the difference in mean number of corpora albicantia between spring and fall third year females in 1967 is 9.6, this may indicate that only two clutches were produced by that segment of the population that year.

Fragmentary data are available on lizards that presumably were in their fourth breeding season or had completed it. One female, collected 12 May 1965, contained 32 corpora albicantia, and was evidently forming her first clutch with six yolked follicles. Another female, taken 19 May 1966, contained 40 corpora albicantia, and had a first clutch of six yolked follicles. A third female, collected 1 April 1967, contained 31 corpora albicantia and four yolked follicles. No second or third clutch data are available for this age group. Four fall lizards were collected, however, which had high counts of corpora albicantia —58, 51, 56, and 69—which suggests they had successfully completed four breeding seasons. An estimate of reproductive potential for this age group can be obtained from the difference in mean counts of corpora albicantia between spring and fall lizards. The mean number of corpora albicantia in spring lizards was 34.3; that of fall lizards, 54.7, a difference of 20.4. This seems indicative of a progressive increase in reproductive potential with age, as demonstrated above, and suggests clutch sizes of six or more eggs in this oldest group of females.

Persistence of Corpora Albicantia

How long corpora albicantia persist in the ovary is a question that cannot be completely answered. The data presented in Table 4 above, and in Tables 6 and 7 below suggest that in many females, if not all, they persist for the life of the lizard. It was obvious to me that at least two sources of error existed in counting these structures. As yolked ovarian follicles enlarge, the tunica in which the scars lie is progressively stretched thinner, tending to disperse the minute patches of orange-pigmented material (lutein ?) comprising the corpora albicantia. Certainly errors were made in counts from females nearing ovulation. Another certain source of error is related to preservation. All specimens were fixed in 10% formalin and then transferred to 30% isopropyl alcohol, but the duration of fixation varied directly with the amount of material being processed. Some specimens were transferred to alcohol after 24 hr fixation, others remained in the formalin trays for several weeks. It is my impression that corpora albicantia were more vivid orange, and consequently easier to see in specimens fixed for longer intervals in formalin. In view of the known action of alcohols on bright red and yellow pigments, it is highly probable that some corpora albicantia escaped detection due to rapid depigmentation. Upon reexamining some of the 1965 series, which had been in formalin much longer than the subsequent series, and in which corpora albicantia were prominent upon initial examination in winter 1965–66, it was difficult in late 1967 to discern the structures at all. I suspect that the low counts obtained from lizards collected in spring 1966 and 1967, in contrast to counts of the same age groups in fall 1965 and 1966, can be attributed to error in counting due to depigmentation. However, only the difference between 1965 hatchlings, collected in fall 1966 and spring 1967, is statistically significant. This hypothesis is strengthened because 6% of fall lizards in 1965 lacked corpora albicantia following their first breeding season, while 45% of spring lizards in 1966 appeared to lack them before their second breeding season! This type of discrepancy was absent in the other samples (Table 7), in which no significant differences were present between lizards collected in fall and the following spring. In view of the correspondence between estimates of reproductive potential obtained from yolked follicles, corpora lutea, and oviductal eggs on the one hand, and counts of corpora albicantia on the other, I think it is reasonable to conclude that corpora albicantia usually

TABLE 6. NUMBERS OF CORPORA ALBICANTIA IN LIZARDS BY YEAR OF COLLECTION.

	Yr collected		
No. corpora albicantia	1965	1966	1967
After 1st breeding season			
range	4–13	6–13	4–12
$\bar{x}$	8.6	10.8	9.0
% sample without	6	0	0
Before 2d breeding season			
range	2–12	1–12	1–12
$\bar{x}$	7.0	4.8	5.7
% sample without	8	45	0
After 2d breeding season			
range	14–24	16–26	14–25
$\bar{x}$	18.0	19.5	18.6
Before 3d breeding season			
range	18–21	14–17	16–23
$\bar{x}$	19.7	15.7	18.8
After 3d breeding season			
range	26–30	31–35	26–39
$\bar{x}$	27.7	33.0	28.3
Before 4th breeding season (1♀ each yr)	32	40	31
After 4th breeding season			
range		46–58	48–69
$\bar{x}$		52.0	53.5

TABLE 7. NUMBERS OF CORPORA ALBICANTIA IN LIZARDS BY PRESUMED YEAR OF HATCHING.

	Yr hatched					
Yr collected	1961	1962	1963	1964	1965	1966
Spring, 1965						
range	32	18–21	2–12	0		
$\bar{x}$	32	19.7	7.0	0		
Fall, 1965						
range		26–30	14–24	4–13		
$\bar{x}$		27.7	18.0	8.6		
Spring, 1966						
range		40	14–17	1–12	0	
$\bar{x}$		40	15.7	4.8	0	
Fall, 1966						
range		46–58	31–35	16–26	6–13	
$\bar{x}$		52.0	33.0	19.5	10.8	
Spring, 1967						
range			31	16–23	1–12	0
$\bar{x}$			31	18.8	5.7	0
Fall, 1967						
range			48–69	26–39	14–25	4–12
$\bar{x}$			53.5	28.3	18.6	9.0

persist for life in this species, and form a useful alternative method for estimation of reproductive potential and population structure.

FOLLICULAR ATRESIA

Atretic follicles were noted only in lizards collected from July to November, and in March and April. In 1966 these were present in 19% of first year and 5% of second year lizards, while in 1967, 22% of each age group contained atretic follicles. Seldom was more than one atretic follicle present per ovary, except in August lizards where presence of yolked follicles less than 2 mm in diameter often suggested that a normal clutch of three or four eggs was undergoing atresia. Atretic follicles were easily distinguished from corpora albicantia as they remained pale yellow during resorption, while corpora lutea turned orange at a diameter of about 1 mm, as described above.

COMPARATIVE PRODUCTIVITY OF RIGHT AND LEFT OVARIES

In first year lizards, the total productivity of the right ovary versus the left ovary was as follows: clutch 1—right 153, left 112; clutch 2—right 71, left 64; clutch 3—right 25, left 29; all clutches—right 249, left 205. Among older lizards, total productivity of the two ovaries was: clutch 1—right 287, left 274; clutch 2—right 120, left 117; clutch 3—right 17, left 16; all clutches—right 424, left 407. Despite the apparently greater activity by the right ovary, no significant differences were found between the two ovaries.

INTERUTERINE MIGRATION OF OVA

Interuterine migration of ova can be demonstrated only when odd numbers of ova are present in the oviducts. Presence of unequal numbers of corpora lutea in an ovary and eggs in the corresponding oviduct are evidence that ova have migrated from one ovary to the opposite oviduct. Among 23 first year females with oviductal eggs, one (4.4%) had two eggs in the right duct with one corpus luteum in the right ovary, and one egg in the left duct with two corpora lutea in the left ovary. This was a third clutch female. Among older females, seven

Table 8. First Clutch Size in Comparison to Female Size and Age.

No. corpora albicantia	N	Snout–vent length (mm) range	Snout–vent length (mm) x̄	No. eggs in 1st clutch range	No. eggs in 1st clutch x̄
0	21	45–49	47.3	1–3	1.9
(1st yr)	23	50–54	51.3	1–4	2.0
1–12	21	54–58	56.5	2–5	3.9
(2d yr)	21	59–63	60.2	2–6	3.8
14–23	3	55–59	57.4	3–4	3.7
(3d yr)	6	60–64	61.9	4–6	5.2
Total	95				

of 31 (22.6%) with oviductal eggs showed evidence of ova migrating to the duct opposite their ovary of origin. Direction of migration was left ovary to right duct in six of the seven females. Two were first of the season; the remainder were second clutches.

Oviposition of Partial Clutches

Three females contained evidence of partial oviposition. In each, six corpora lutea of approximately equal size were present. One contained four oviductal eggs, the other two five eggs each, indicating partial clutches of two in the first instance and one each in the second. One was a second year female, two were third year females, and in each case it was the first clutch.

Clutch Size in Relation to Body Size and Presumed Age

Relationship of first clutch size to female age is presented in Table 8. The criterion for age estimation is the number of corpora albicantia present: 0—first year; 1–12—second year; 14–23—third year.

Within first and second year age groups there is no increase in clutch size with increasing body size. Between the two groups, however, there is an increase, nearly two-fold, in clutch size. Data on third year females are interesting but inadequate for meaningful comparison. Overall clutch size relative to female body length is presented in Table 9. Data obtained by Ishihara (1964) from captive lizards in the Kansai region of Japan (Kyoto) are included for comparison. Ishihara's estimates are based upon 274 clutches oviposited by captive lizards. As he gave no information which would clarify his methods of measurement, I have assumed that he grouped his

Table 9. Overall Clutch Size Relative to Female Body Size in Kanto and Kansai[1] Populations.

	♀ body size classes (mm) 45	50	55	60	65	Total clutches
No. clutches						
Kanto	54	88	97	82	11	332
Kansai	12	66	116	71	12	274
No. ova						
Kanto	136	243	366	328	49	
Kansai	37	210	388	257	51	
x̄ clutch size						
Kanto	2.5	2.8	3.8	4.0	4.5	
Kansai	2.8	3.2	3.3	3.6	4.3	
Kanto—13%	2.2	2.4	3.3	3.5	3.9	
% comprised of total clutches						
Kanto	16	27	29	25	3	
Kansai	4	24	42	26	4	

[1] Data from Ishihara, 1964.

lizards in classes to the nearest 5 mm, and this was done in analyzing my data. My overall estimates are based upon counts of yolked follicles, corpora lutea and oviductal eggs from 332 clutches. As there is an average difference of 13% between the overall estimates and that obtained from counts of oviductal eggs alone, an estimate reduced by 13% is also given.

Data presented in this manner clearly indicate an increase in clutch size with increased female body length.

Clutch and Egg Size and Weight in Relation to Female Age

Among several hundred lizards maintained in the laboratory during the study, many females oviposited during the breeding season. While these lizards were not from the Hanno study population, they were all collected within about 30 km of Hanno, most of them coming from the same Tokyo suburb. It was possible to obtain accurate size and weight data for 25 clutches. Among these, year of hatching could be estimated by corpora albicantia for 20 females. Data are presented in Table 10.

Most clutches were probably second or third of the season, to judge by the dates of oviposition, which ranged between 9 June and 13 July. Because of the small samples available, statistical comparison was not at-

TABLE 10. COMPARISON OF CLUTCH AND EGG SIZE AND WEIGHT.

♀ age (yr)	N	body size (mm)		clutch size		total clutch wt (g)		egg size length (mm)		egg size width (mm)		egg size wt (g)	
		range	x̄	range	x̄	range	x̄	range	x̄	range	x̄	range	x̄
1	9	47–51	48.5	3–4	3.3	0.517–0.986	0.737	8–12	9.4	5–6	5.5	0.119–0.305	0.199
2	9	53–64	57.6	3–9	5.1	0.621–2.246	1.129	8–11	9.5	5–7	6.1	0.150–0.280	0.221
3	2	59–60	59.5	4–5	4.5	1.221–1.422	1.322	10	10.0	7	7.0	0.258–0.306	0.294

tempted, but the data suggest deposition of heavier clutches by older females. In only four females was post-oviposition weight recorded. One, a first year female (s-v 47 mm) deposited three large ova weighing .894 grams, or 50.4% of her post-oviposition weight (1.77 g). Two second year females weighing 3.34 and 2.98 g post-oviposition, deposited clutches with weights of 1.065 and .941 g respectively, or 31.9 and 31.6% of their weights. One third year female (3.54 g), deposited a clutch weighing 1.422 g, or 40.2% of her post-oviposition weight.

DURATION OF INCUBATION PERIOD AND HATCHLING SIZE

Eggs from the above clutches were placed in tightly covered plastic containers in which a hardened mixture of charcoal and plaster of Paris covered the bottom for a depth of one-half to one inch. When visible condensation disappeared from the sides of the containers, a small quantity of water was added. Room temperature was maintained between 25 and 28° C. Although many eggs succumbed to mold, enough hatched to furnish adequate data on incubation time and hatchlings. Egg required 32–38 days (x̄, 34.2 days) from oviposition to hatching, and hatchlings varied in snout–vent length from 21 to 24 mm (x̄, 22.5 mm). Their weights, within one day of hatching, averaged .214 grams, with a range from .179 to .269 grams.

POPULATION STRUCTURE

Sex ratio.—The numbers of lizards collected, by sex during the period 1965–67 are presented in Table 11.

With chi square testing, no significant differences were found between sexes in any of the above samples. Sex ratio in all age groups sampled for each season, was 1 : 1.

Structure of total sample.—Specimens collected from all five sites during fall and spring of each year were used to determine the total sample structure. Those collected during the reproductively active periods from the last three weeks of June throughout July were excluded, as regression of corpora lutea into corpora albicantia in this period was considered to increase error in estimating age of females. Of 184 females, 115 (62.5%) had survived their first breeding season; 46 (25.0%), their second; 18 (9.8%), their third; and 5 (2.7%), their fourth.

Structure in two individual paddy fields.—Sites 1 and 2 were sampled most intensively for the entire three years: 94 adult females from site 1 and 99 adult females from site 2 comprise the samples compared in Table 12.

A three year estimate of population structure in sites 1 and 2 is presented in Table 13.

In spring, then, one might expect the adult female population to be comprised of approximately 80% entering the second year's breeding season, 15% into the third year, and 5% approaching their fourth year. In fall, adult females would include 60% survivors of the first breeding season, 28% from the second, 10% from the third and 2% or so which had oviposited for four seasons.

DISCUSSION

Several recent studies present data on the ovarian cycle and reproductive potential of

TABLE 11. NUMBERS AND SEX OF LIZARDS COLLECTED 1965–67.

Period	No. 1st yr ♂	No. 1st yr ♀	No. older lizards ♂	No. older lizards ♀
Mar.–July 1965	47	45	23	25
Aug.–Nov. 1965	44	41	28	37
Mar.–July 1966	81	75	74	58
Aug.–Nov. 1966	29	26	29	15
Mar.–July 1967	85	81	61	44
Aug.–Oct. 1967	41	35	60	50
Totals	327	303	275	229

TABLE 12. COMPARISONS BY HATCHING YEAR OF SAMPLES FROM PADDIES 1 AND 2.

Sample	Proportion (%) of sample hatched in year					
	1961	1962	1963	1964	1965	1966
Mar.–June 1965						
Paddy 1		40.0	60.0			
2	12.5	12.5	75.0			
July–Oct. 1965						
Paddy 1		10.0	16.0	74.0		
2		9.0	32.0	59.0		
Mar.–June 1966						
Paddy 1		7.0		93.0		
2			6.0	94.0		
July–Oct. 1966						
Paddy 1		9.0	18.0	18.0	55.0	
2			9.0	24.0	67.0	
Mar.–June 1967						
Paddy 1			6.0	18.0	76.0	
2				8.0	92.0	
July–Oct. 1967						
Paddy 1				14.0	50.0	36.0
2				11.0	21.0	68.0

TABLE 13. THREE YEAR ESTIMATE OF POPULATION STRUCTURE IN PADDIES 1 AND 2.

Lizards surviving to age (yr)	July–Oct.		Mar.–June	
	paddy 1 %	paddy 2 %	paddy 1 %	paddy 2 %
1	54	65	79	89
2	31	26	17	8
3	13	9	4	3
4	2	0	0	0

lizard species with seasonally restricted reproduction. The most valuable of these, in terms of variety of data presented, is that of Tinkle (1961) on *Uta stansburiana*. Less complete information on ovarian cycles has been published by Woodbury and Woodbury (1945) on *Sceloporus graciosus*; Johnson (1960), *Holbrookia texana*; Mayhew (1963, 1965, 1966a, 1966b) on *Sceloporus orcutti*, *Uma inornata*, *U. scoparia*, and *U. notata*, respectively; Hoddenbach (1966), *Cnemidophorus sexlineatus*; and McCoy and Hoddenbach (1966), *Cnemidophorus tigris*. Estimates of reproductive potential have been made by Blair (1960) for *Sceloporus olivaceus*. With reference to *T. tachydromoides*, only Ishihara (1964) has provided useful information. The study by Inukai (1930) contains factual errors that diminish its value, while Minobe (1927) made only general reference to breeding habits.

As described above, follicles of hatchling *Takydromus* increase in numbers and size as they grow, reaching minimum size for yolk deposition in late spring following their first hibernation. Juveniles approaching maturity have one-third to one-half as many follicles as older lizards. By contrast, older females enter hibernation with unyolked follicles at a maximum in size and numbers. Tinkle (1961) found follicles present in hatchling *Uta* and an increase in mean number of follicles as size increased. Minimum numbers and size of follicles are present in *Takydromus* at the close of the breeding season, and in *Uta* there is a slight decrease in mean number just after ovulation. Johnson (1960) found no change in follicle numbers throughout the season among adult *Holbrookia*. Mayhew's data (1963, 1965, 1966a, 1966b) are more difficult to interpret because he used the term "ovarian eggs" instead of follicles, and he failed to distinguish between yolked and unyolked follicles. With *S. orcutti* and *U. notata*, Mayhew found more ovarian eggs in adults than in juveniles, while in *U. scoparia* there was a tendency toward increased numbers of ovarian eggs from March to July, but a decrease thereafter. In *U. inornata* few ovarian eggs were present in late summer.

Yolk deposition in *Takydromus* juveniles begins when they reach a snout–vent length of 41–50 mm, usually in late May, while in adults, most females (85%) newly emerged from hibernation in late March possessed yolked follicles, although none collected in late October and early November had yolked follicles (Fig. 5). Evidence of pre-hibernation vitellogenesis in another population will be presented in a future study, and this may be the explanation for these observations. Woodbury and Woodbury (1945) stated that yolk deposition in *S. graciosus* begins in the summer and fall of the year before oviposition, a very different situation than described for the other species cited here, in which yolk deposition occurs immediately following hibernation (*Cnemidophorus*) or in early and middle spring (*Uta*, *Uma* spp., *S. orcutti*). Deposition of yolk in follicles destined for successive oviposition occurs uncommonly in *Takydromus* and in *C. sexlineatus*, but more often after ova have entered the oviducts, as

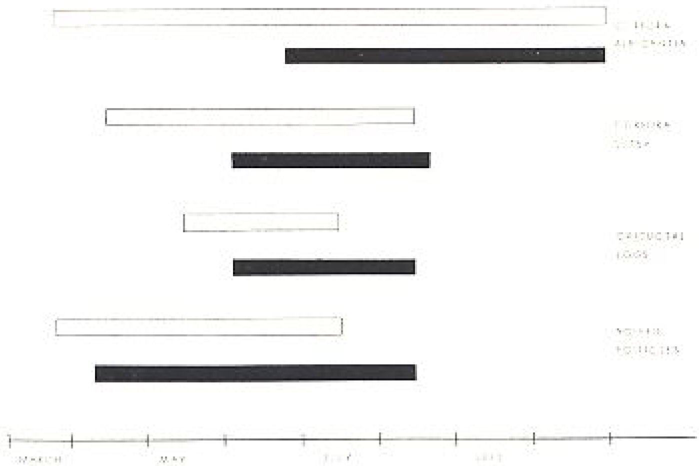

Fig. 5. Reproductive patterns of female *Takydromus tachydromoides*. Solid bars, first year lizards; hollow bars, older lizards.

in the three *Uma* species, *Holbrookia*, *C. tigris*, and, rarely, *Uta*.

The maximum size attained by yolked follicles, 6.8–7.6 mm in *Takydromus* provides an indication of size at ovulation, similar to that described for *Uta* (7–8 mm), and *S. graciosus* (7 mm), but smaller than that reported for *H. texana* (9.2–10 mm), and *Cnemidophorus* (10–12 mm).

Takydromus is unique among the species here considered in having corpora lutea persisting as bright orange corpora albicantia for life. In *H. texana*, corpora lutea are not absorbed completely until winter, well after the last ovulation in August. Here too the small corpora lutea are bright orange, due possibly to a concentration of lutein pigment. Johnson (1960) also found no evidence of differential rates of absorption of corpora lutea for successive clutches. In *Uta*, *S. orcutti*, *C. tigris*, and the *Uma* species, corpora lutea remain prominent prior to oviposition, but disappear rapidly thereafter.

The persistence of corpora albicantia provides a valuable means of age estimation for individual females and permits an estimate of population structure that I believe to be quite accurate. How widespread this phenomenon may be remains to be seen, but in at least one other species, *Takydromus smaragdinus*, corpora albicantia are present prior to onset of oviposition in the spring (Telford, unpubl. data). Why no mention of corpora albicantia is made in the literature dealing with *Takydromus* is difficult to understand, in view of the prominence of these structures in the ovaries. Inukai (1930: 34) claimed to have studied more than 6000 *Takydromus* during a six year period, and to have determined the number of eggs by dissecting 320 females. He further commented ". . . we always find in the ovary after egg laying as many corpora luteum as the number of eggs laid." His failure to mention the presence of bright orange scars indicates to me superficiality of observation. This explanation is reinforced by another comment: ". . . mating is repeated to some extent during the breeding season . . . but the spawning of the eggs takes place just once throughout the season." Other errors exist in this paper, especially with regard to oviposition site: "*Takydromus* neither digs the ground for the egg-deposition nor covers the eggs with soil or anything after spawning." My observations agree with Minobe (1927:548), who stated that the eggs ". . . are invariably covered with soils. The mating and spawning appear repeated for certain times throughout the season."

Good agreement on clutch size is shown in Table 13, where comparison is made between data published by Ishihara (1964:table 2) and that presented herein. The greatest differences lie in the estimates for smaller (first year) females, which are 20–25% higher in the Kansai lizards. I suspect this may be due to collecting bias by Ishihara, as he probably emphasized the capture of obviously gravid females, and purposely may not have included many small first year lizards in his laboratory colony. The difference in esti-

TABLE 14. INDIRECT ESTIMATE OF CLUTCH NUMBER.

Yr	Reproductive season		Formation of 1st clutch		Estimated No. clutches	
	dates	days	dates	days	Telford interval	Ishihara interval
1st yr ♀						
1965	15 May–10 Aug.	86	15 May–20 June	35	2.5	4.9
1966	15 May– 1 Aug.	76	15 May–10 June	25	3.0	4.3
1967	20 May–10 Aug.	81	20 May–15 June	25	3.2	4.6
Older ♀						
1965	10 Apr.–1 Aug.	112	10 Apr.–20 May	40	2.8	6.4
1966	30 Mar.–1 Aug.	122	30 Mar.–20 May	50	2.4	7.0
1967	25 Mar.–1 Aug.	127	25 Mar.–20 May	55	2.3	7.3

mates for the largest size group cannot be evaluated due to the very small sample sizes available to both of us. Clutch sizes are given by Ishihara (1964) as 1–8, by Minobe (1927) as 2–9, and by Inukai (1950) as 1–9. Among Hanno lizards, clutch size ranged from one to seven, but a single clutch of nine was deposited by a lizard in my laboratory colony.

The principal difference between my study and that of Ishihara lies in the number of clutches per female per season. I have no good evidence of more than three clutches, as far as could be determined by examination of ovaries. Ishihara found about 9% of his lizards laying more than three clutches per season: five deposited four, two laid five, and one, six clutches! He found the average clutch number was two, which I calculate from data in his Table 1 to actually be 2.4 clutches per female. If I take the mean number of ova per clutch produced by my females in each season, as estimated by all methods (Tables 3, 6, 8), and divide this figure into the mean number of corpora albicantia in fall lizards of the appropriate age groups (Tables 4, 7, 9), I find an overall mean of 2.9 clutches per female in one season, with a range among all age groups from 1.8 to 4.2 clutches. Further analysis indicates overall averages per age group as follows: first year, 3.2–4.2, $\bar{x}$ 3.7; second year, 1.9–3.0, $\bar{x}$ 2.6; third year, 1.8–3.5, $\bar{x}$ 2.4 clutches. With respect to clutch number, I do not think there is a real difference between my findings and those of Ishihara, in view of the different approach.

An indirect method for estimating clutch number was used by Tinkle (1961:229). He calculated the length of the reproductive season and then estimated the time required to produce the first clutch from inception of follicle enlargement until most had oviductal eggs. By dividing the length of the reproductive season by the time required to produce the first clutch, he arrived at estimates of clutch number. This procedure has been used here, modified by the difference in length of reproductive season for first year and older females. The data are presented in Table 14, along with an estimate of clutch number derived from using Ishihara's mean interval of 17.5 days between successive clutches of captive females.

By this method, there is an overall mean number of 2.7 clutches. This is similar to the overall mean of 2.9 given above by use of mean clutch size and number of corpora albicantia. Arguments presented by Tinkle in behalf of his method are appropriate here. As to the results from use of Ishihara's mean interval between clutches, I can only comment that here again is illustrated the danger inherent in using captive lizards to describe ecological parameters of populations.

Evidence of multiple clutches for the species they studied was presented by the following workers: Johnson (1960), four clutches of five eggs each, for a reproductive potential of 20 ova annually in *H. texana*; three clutches in *U. stansburiana* by Tinkle (1961), for a potential of 9.0–17.1 ova per female, depending upon body size; two clutches of 2.2 ova each for a reproductive potential of 4.5 eggs in Texas *C. tigris* by McCoy and Hoddenbach (1966); and a maximum of four clutches per female yearly in *S. olivaceus* by Blair (1960), with 8–30 eggs per clutch. Data on other species have been summarized by Tinkle (1961:229), who has commented on the difficulties encountered in comparing information on lizard reproductive potential available in the literature. In *S. olivaceus*, reproductive potential increases with age as both clutch size and number are increased. The reproductive potential of *Takydromus* also increases with age, but this results from larger clutches alone. In *C. tigris*, the increase in reproductive potential with age also results from greater clutch size in older females.

Follicular atresia was recorded in 5–22% of *Takydromus* females in the pre- and post-ovipositional seasons, but not during the active reproductive period. Both Hoddenbach (1966) and Tinkle (1961) noted atresia occurring within the active season, but Hoddenbach presented no evidence to support his suggestion that accessory yolked follicles are resorbed prior to ovulation in *Cnemidophorus*. Tinkle estimated that 8–10% of enlarged follicles undergo atresia, thus accounting for the difference in clutch size estimated by yolked follicles and by corpora lutea-oviductal eggs. In *Takydromus*, I think atresia is the fate of follicles which begin yolk deposition too late in summer to complete the cycle. Probably any yolked follicle less than 2 mm in August or even in late July will become atretic. Those atretic follicles present in early spring appear to be remnants of the previous summer's cycle, as they were found only in older females. I could not detect atresia during the active season, nor was it feasible to estimate the percentage of enlarged follicles meeting this fate.

In *Takydromus*, the right ovary seemed more productive than the left, but differences lacked significance. Inukai (1930) also found that the right ovary ". . . prevails a little over the left." The same impression was recorded by Mayhew for *U. notata* (1966b) and *U. scoparia* (1966a) with no statistical significance present. He also found no difference between ovaries of *U. inornata* (1965). In *S. orcutti*, however, Mayhew (1963) found a significantly higher number of ovarian eggs in the right ovary among his immature individuals and his total sample, but not among the adult sample. Johnson (1960) reported an equal number of oocytes in each ovary in 96% of his *H. texana* females.

Interuterine migration of ova in lizards has been documented by Tinkle (1961), Mayhew (1963, 1965, 1966a, 1966b), and Hoddenbach (1966). In *U. stansburiana*, migration occurred in 20% of the sample, more commonly from left ovary to right duct. It was found in 23% of *U. notata* females, in 9% of *U. scoparia*, and in 13% of *U. inornata*, according to Mayhew (1965, 1966a, 1966b). Mayhew (1963) also found evidence of migration in three of four female *S. orcutti* with oviductal eggs. Hoddenbach's citation of a 60% migration rate in *C. sexlineatus* is hardly justified, being based upon a sample of only five females. He suggested that the stomach's position on the left side might influence migration from the left ovary to the right oviduct, a reasonable explanation. In *Takydromus*, direction of migration was usually left to right, and was more common in older females (22%) than in younger (4%), possibly as a consequence of larger clutch size in the former group.

Evidence of oviposition of partial clutches was found by Johnson (1960) in *H. texana* (27%), and by Mayhew (1966b) in *U. notata* (9%), but only rarely by Tinkle (1961) in *Uta*. Hoddenbach (1966) stated that the entire clutch of *C. sexlineatus* is deposited at once. I found partial clutches oviposited by *Takydromus*, but in only three females, less than 1% of the sample. Inukai (1930:37) stated that all eggs were deposited at once unless the animal was disturbed. Although Ishihara (1964) apparently did not consider this factor, it is possible that some of his clutches (in excess of three per female) represent partial ovipositions by captive females.

A correlation probably exists between the age at sexual maturity and size attained by the species, or more likely, its growth rate. Tinkle (1961:215) presented estimates of age at maturity for several species of lizards. Almost all Hanno *Takydromus* reproduce the first summer following hatching: 97% of fall lizards over 50 mm contain corpora albicantia. Some are large enough by April for yolk deposition, most by late May, but a few not until late July. As hatchlings appear from mid-July to mid-October, and most commonly in September, attainment of sexual maturity at an age of eight or nine months is suggested. Although a future study will deal with interpopulation variation in age at maturity, I should mention that this is not characteristic for all *Takydromus* populations (some hatchlings mature much more rapidly in the Tokyo area). I have no data on Hokkaido *Takydromus*, but would suggest that these must possess interesting characteristics of metabolism, growth, and reproduction in view of the extremely short (three months?) annual active period.

It is generally stated that increases in re-

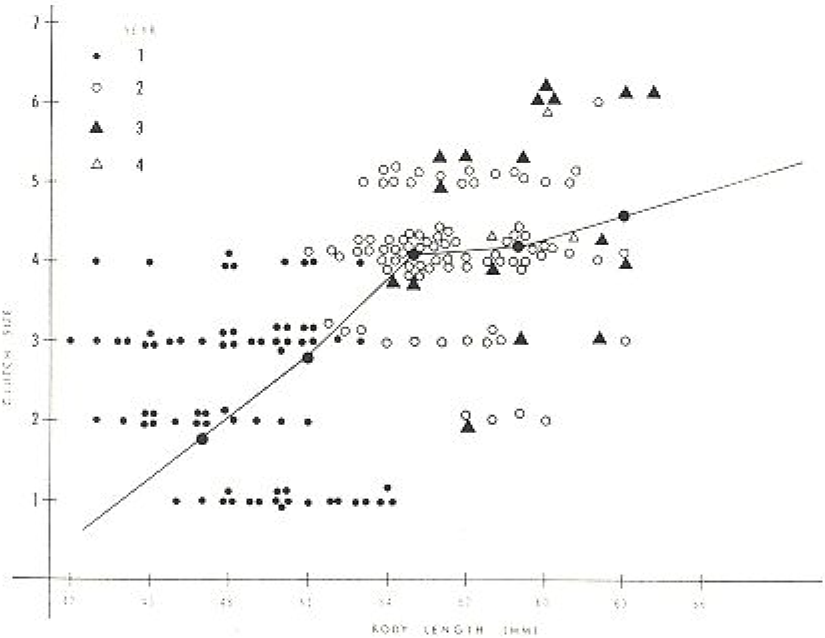

Fig. 6. Clutch size in correlation with female body size. Regression line calculated.

productive potential are due to increasing body size, and usually data have supported this contention. Hoddenbach (1966) and Johnson (1960) found no differences in clutch size of *C. sexlineatus* and *H. texana* respectively, with increase in body size. In *C. sexlineatus* the sample size was inadequate, in my opinion, to justify the conclusion drawn. Tinkle found an increase in reproductive potential with increase in mean size of females. He stated, however (1961:227), that the biggest increase was among lizards of the largest size group. Although he did not consider this point in view of his data supporting an annual turn-over of the *Uta* population, it is possible that this largest age group (about 11% of his sample), is comprised of females in their second breeding season. Blair (1960:94, 97) considered clutch size to be a function of both size and age of females, but he did not present data which would demonstrate differences in clutch size between small and large females in the same age group. I have shown in Table 8 and Fig. 6 that there are no differences in clutch size between small and large lizards within the same age group, yet between the largest first year lizards and smallest second year lizards, clutch size nearly doubles. My unpublished data demonstrate considerable differences in food reserves as determined by proportionate liver and fat body weights among females of different age groups. In *Takydromus*, the apparent increase in clutch size with greater body size may result from availability of proportionately larger food reserves in older lizards.

Tinkle (1961:228) had the impression that eggs of small clutches were larger with more yolk than eggs from larger clutches. The data of Table 10 indicate that this is not the case in *Takydromus*, but instead older females with larger clutches produce heavier eggs. This again may be a result of proportionately greater food reserves in older females.

In this study, an incubation period of 32–38 days ($\bar{x}$, 34.2) was reported for *Takydromus* eggs in a room where ambient temperature varied between 25° and 28° C. Minobe (1927:548) reported an incubation period of 42 days and Inukai (1930:39) over 50 days. Ishihara (1964:table 4) found a mean incubation period of 35.9 days at a mean temperature of 27.5° C, or very close to my results. Ishihara also found that when eggs are kept between 23° and 29° C, hatching occurs about three days earlier for each one degree rise in temperature; temperatures of 15° and 34° C are fatal to development. Ishihara's data on mean egg size (9.3 × 6.0 mm) are similar to mine (Table 10), but his extremes are greater with respect to width: 7.5–11.5 mm by 5.0–9.0 mm. His average egg weight, 0.21 g, lies between my figures of .199 g for first year females, and .221 g for second year clutches, but far short of weights for eggs of third year females (.294 g). Ishihara gave only hatchling total length, so comparison is not easily made, but he stated a mean hatchling weight of 2.42 g, an obvious typographical error. A figure of 0.242 g would lie within my extremes of .179 g and .269 g ($\bar{x}$, .214), for hatchling lizards.

Ishihara found a sex ratio of 1:1 among hatchlings, and later stated (pers. comm.) that the ratio does not change with time. My findings agree completely. Although Ishihara has not presented other data on population structure, the size grouping similarities of our respective samples (Table 9) suggest that there would be no great difference between our populations. As expected, first year females are the largest age group in the *Takydromus* breeding population. In a hypothetical sample of 100 females from the Hanno population, 62.5 would be first year, producing an average of 7.4 eggs each, for a total of 462; 25 would be second year, producing 11.4 eggs each, with a total of 285; 9.8 would be third year, averaging 12.8 eggs apiece, and a total of 125; and 2.7 might be fourth year, producing 20.4 eggs each, for a total of 55. One would expect a total egg production by these 100 females of 927 eggs in one season, nearly 50% of which would come from first year lizards, and about 80% from lizards in their first two years. Clearly, any drastic change in environment, such as a prolonged, severe winter which arrived early and remained late, would have a pronounced effect upon population density in subsequent years. Climatic factors alone probably increase the importance of second year females to the population and reduce the net contribution of first year lizards well below that indicated by egg production estimates.

Summary

A population of the Japanese lizard *T. tachydromoides* in central Honshu was sampled monthly from March to November in 1965, 1966, and 1967.

Ovarian follicles increase in number and size from hatching (mid-July to mid-October) until hibernation in November, when growth ceases until after emergence in March. Yolk deposition in first year females begins eight or nine months after hatching, when the lizard attains a body length of 41–50 mm, and when follicles reach 1.0 mm in size. Most older females collected in late March, during emergence from hibernation, contained yolked follicles. Maximum diameters of yolked follicles in first year and in older females were 7.6 mm and 6.8 mm, respectively. Yolked follicles 2 mm or less in August lizards probably are destined for atresia. Deposition of yolk in follicles presumably belonging to different clutches was found in less than 10% of the sample.

Oviposition of first year lizards begins in early June, reaches its maximum in July, and terminates before mid-August. Older females begin oviposition in early May, reach their peak in the first half of June, and cease laying in late July. Rarely, clutches may be deposited in April.

Follicular atresia was observed in a maximum of 22% of the lizards collected in fall and spring. No atretic follicles were seen during the active reproductive season.

No significant differences were found in comparing productivity of right and left ovaries, although the right ovary seemed to be more active.

Interuterine migration of ova occurred in 4.4% of first year and 22.6% of older females, with direction of migration almost always from left ovary to right oviduct. Three females (< 1%) contained evidence of oviposition of partial clutches.

Corpora lutea regressed in experimental lizards from an average size of 2.1 mm on the day of oviposition to 1.0 mm in all females killed five days and more post-oviposition. Mean size of corpora lutea in females containing oviductal eggs was 2.4 mm (1.9–3.0 mm). The colors changed during regression from reddish (corpora haemmorhagica) through cream, white or yellow (corpora lutea) to bright orange (corpora albicantia). Corpora albicantia apparently persist for life, and permit segregation of females into age groups that are probably more accurate than age groups based upon body size.

Estimates of age groupings by corpora albicantia counts in pre- and postoviposition lizards suggest that first year lizards contain no corpora albicantia in spring and 4–13 in fall; second year lizards, 1–12 in spring and 14–26 in fall; third year, 14–23 in spring and

26–39 in fall; and fourth year, 31–40 in spring and 51–69 in fall. The incidence of corpora albicantia in adult lizards collected from 15 August until hibernation is 97%.

Estimates of clutch size are similar when obtained by using yolked follicles, corpora lutea, or oviductal eggs. Clutch size of first year lizards ranges from 1–4 for all clutches, with means of 2.6 for the first clutch and 2.4 for the second and third. Clutches of second year females range from 1–6, with means of 4.0 for the first and second clutches, and 3.4 for the third clutch. Third year females lay clutches of 1–7 ova, with means of 4.4 and 5.1 for first and second, respectively. Meager data suggest third clutches of 3.5 eggs. Fourth year females evidently form clutches of 4–6 ova, or more.

Mean clutch number, calculated by dividing the average number of ova per clutch into the mean number of corpora albicantia in fall lizards, is 2.9. Dividing length of the reproductive season by time required to produce the first clutch suggests an overall mean clutch number of 2.7. The reproductive season, or that period marked by the first appearance of yolked follicles until oviposition ceases, varied during the three years from 76–86 days for first year females, and from 112–127 days for older females.

Estimates of reproductive potential were obtained by two methods: 1) from an average of counts of yolked follicles, corpora lutea, and oviductal eggs, with the assumption that three clutches are produced per season, and 2) from the mean difference between counts of corpora lutea in spring and fall lizards. The mean reproductive potential of first year lizards is 7.4 (method 1) and 9.3 (method 2): second year lizards, 11.4 (method 1) and 12.9 (method 2): third year lizards, 12.8 (method 1) and 11.6 (method 2). Differences in corpora albicantia counts between spring and fall fourth year lizards suggest a mean reproductive potential of 20.4.

There is no difference in average clutch size between small and large females of the same age group, but second year females produce first clutches nearly twice as large as those of first year lizards. Average weight of individual eggs and total clutches increases as females age. Total clutch weight ranges from 30 to 50% of the females postovipositional weight. Eggs incubated between 25° and 28° C required 32–38 days for hatching, and hatchlings varied from 21 to 24 mm ($\bar{x}$, 22.5 mm) snout–vent length. Hatchlings weighed from .179 to .269 g, averaging .214 g.

The sex ratio in all age groups per season is 1:1. Of the total adult female sample, 62.5% survived their first breeding season, 25.0% their second, 9.8% their third, and 2.7% their fourth season.

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